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A Shelf Plankton Model: Description and Testing

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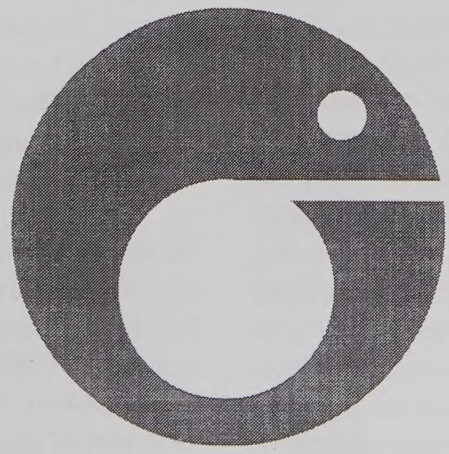

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A Shelf Plankton Model: Description and Testing

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Introduction

A previous report (Steele and Henderson, 1976) described development of a simulation model to portray the response of a nutrient, phytoplankton, zooplankton (N/P/Z) system to vertical mixing in the water column. At that time there were no physical models that gave realistic descriptions of the time-varying processes responsible for vertical mixing. Since then these models have been developed; specifically by Price *et al.* (1986).

There are, however, a number of technical problems in adapting this model - or others - to continental shelf environments, and combining it with N/P/Z biology. This report describes these problems; the solutions adopted for the particular problems of shelf physics; and the methods for coupling the physical and biological components.

The technical development of the simulations required testing of the physics with 10 years of wind data - the main time-varying forcing function. Also the biology required testing of the vertical structure of N and P with data from ICES archival sources that gave profiles of temperature, nitrate, and chlorophyll.

The application of the combined physical/ biological model is to general ecological questions (Steele and Henderson, 1995) and to simulation of results from FLEX (Henderson and Steele, 1995). This report provides the necessary basis for these papers in terms of the technical solutions used in the simulations, and the data used to develop and test these models.

Background

One-dimensional models of vertical mixing (eg Price *et al.*, 1986) have been able to provide realistic simulations of thermocline structure over seasonal time scales (Martin, 1986). Such models of the physics of the upper ocean can be combined with one-dimensional models of nutrient cycling through the plankton to simulate vertical profiles and the flux of nutrients and plant carbon through the thermocline (Spitzer and Jenkins, 1989).

There is one significant difference when a solid bottom is introduced. The boundary condition for heat flux is zero, whereas there is a flux of particulate nitrogen into the bottom and a flux of soluble nitrogen out. This difference is particularly important in deeper stratified locations such as the Fladen Ground (120-150 m) in the middle of the northern North Sea where the deeper temperatures (75 m-bottom) are uniform with depth and change relatively little until the overturn in the autumn (Fig. 1). This temperature condition does not require any assumptions about deep-water turbulence. However, the nutrient flux from the benthic boundary layer into the water column does require deep-water mixing. For a stratified water column, in spring and summer, wind-induced mixing is negligible below the thermocline. Thus, regenerated nutrient would be concentrated near

the bottom. This is not observed and thus, a significant rate of mixing is required to transfer nutrient into the water column beneath the thermocline.

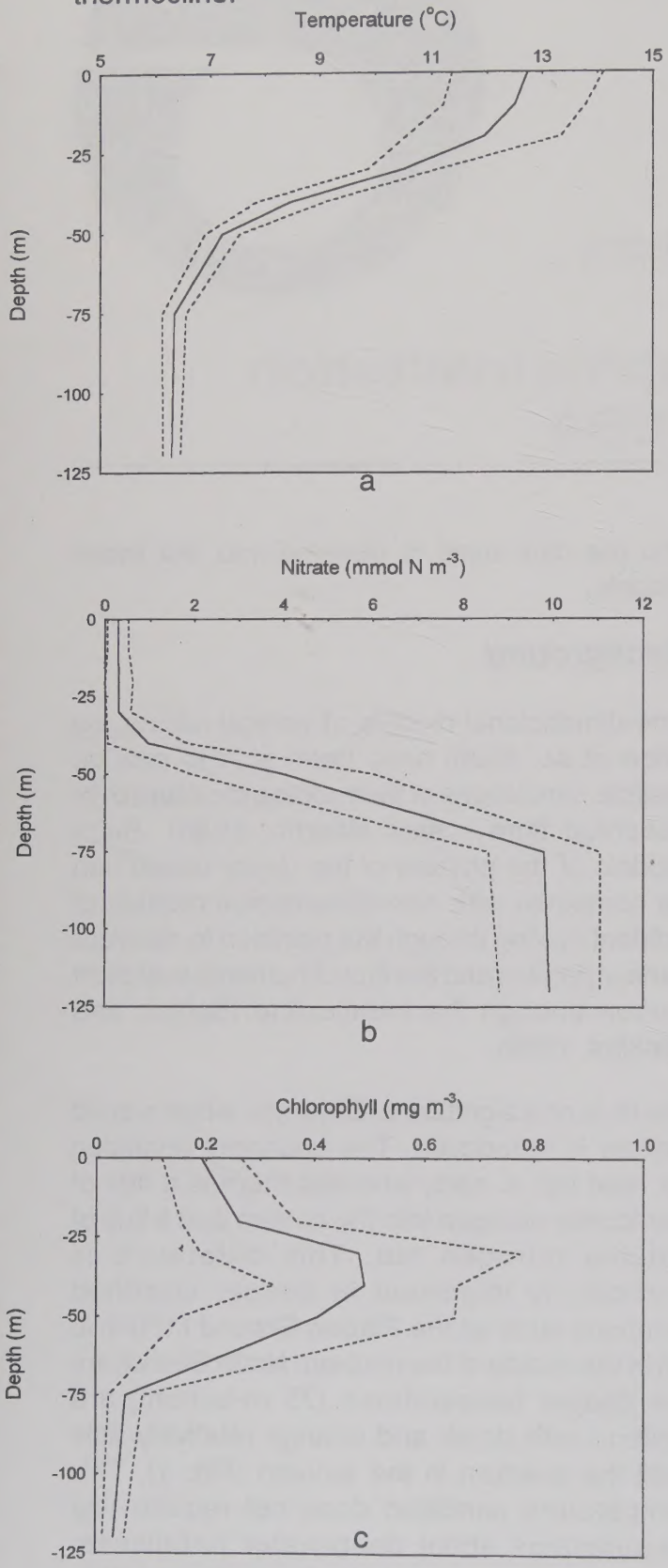


Figure 1 Mid-summer profiles on the Fladen Ground in the northern North Sea. Data from ICES archives for 1976-85; days 150-250 a) temperature; b) nitrate; and c) chlorophyll showing the mean and ra

The vertical distribution of mixing is also relevant to another parameter. The mid-water chlorophyll maximum is a pervasive feature of nutrient limited, stratified water columns. The ability of simulations to reproduce this feature can be regarded as a basic diagnostic test. A uniformly high rate of vertical mixing throughout the water column will eliminate the chlorophyll maximum.

Thus, the wind-induced mixing from the surface needs to be combined with bottom-generated turbulence which decays with distance from the bottom boundary layer. These interactions will be quantified using a modified PWP (Price, Weller, Pinkel) simulation of vertical mixing to drive a 24-layer N/P/Z (nutrient, phytoplankton, zooplankton) model.

Solution of these technical problems provides background to a series of papers dealing with processes on the continental shelf (Steele and Henderson, 1995; Solow and Steele, 1995; Henderson and Steele, 1995). Conditions in the North Sea are used as illustrations. These papers describe the cohort structure in the herbivores, scales of patchiness, and the interannual variability in the North Sea. The simulation of nutrient transfer is kept as simple as possible so that attention can be focused on vertical structure and copepod dynamics. In particular, only one form of nitrogen is assumed and the detailed effects of a microbial pathways, especially in the benthos, are ignored.

Vertical Structure

The data used here (Fig. 1) illustrate the three main features. There is negligible downward mixing of heat to the deepest layers. In consequence, temperature in the deep layers remains relatively constant with time as well as with depth during spring and summer.

Nitrate is also constant with depth over the bottom 50 m, but there is a general increase in this deep water concentration from an average value of 7.9 mmol N m^{-3} in April to10.6 mmol N m^{-3} in August. During this period, primary production will be about

60 gC m^{-2} (Steele, 1974). Assuming that approximately 30% reaches the bottom as particulate, mainly faecal, matter; that the nitrogen content is regenerated with a ratio of 100 mgC to 1 mmol N; and that this is distributed as nitrate over the bottom 50 m, then the increase in concentration would be 4 mmol N m^{-3} which is relatively close to the observed increase. Thus, the biological model will assume that 30% of the phytoplankton C and N grazed is excreted as faecal pellets that fall to the sea bed. This input is necessary to fuel the benthic ecosystem (Steele, 1974). Further, for simplicity, we shall assume immediate regeneration rather than create a benthic component with delay times of 2-4 weeks (Davies, 1975).

Lastly, the observations show that a mid-water chlorophyll maximum is always present in mid-summer. The magnitude and depth can be variable and related to the depth of the nutricline. In this model, it is assumed that this peak corresponds to a maximum in particulate carbon due to a decrease in the phytoplankton sinking rate in the nutricline (Steele and Yentsch, 1960). However, the chlorophyll maximum could also be due, in part, to increases in the chlorophyll to carbon ratio (Steele, 1964; Cullen, 1982).

Vertical mixing

Calculations of the vertical temperature distribution were made using the PWP formulation. The driving forces for the physical model of the vertical structure are a) the average seasonal cycle of radiation for this area taken from the Bunker climate atlas (Isemer and Hasse, 1985); and b) the actual wind data collected by the UK Meteorological Office at the station at Kirkwall on the Orkney Islands for the year 1976. The data for 1976 are used for the ecological simulations in this paper because there was intensive data collection during the Fladen Experiment (FLEX) in the spring of 1976. Figure 2 shows the calculated mixed layer depth for 1976, commencing on day 61, together with the estimated temperature distributions. The calculated main thermocline lies between 30 m and 50 m. The observations (Fig. 1) are more diffuse but the largest gradient is in the same depth range. The maximum observed temperature is close to that in the simulations.

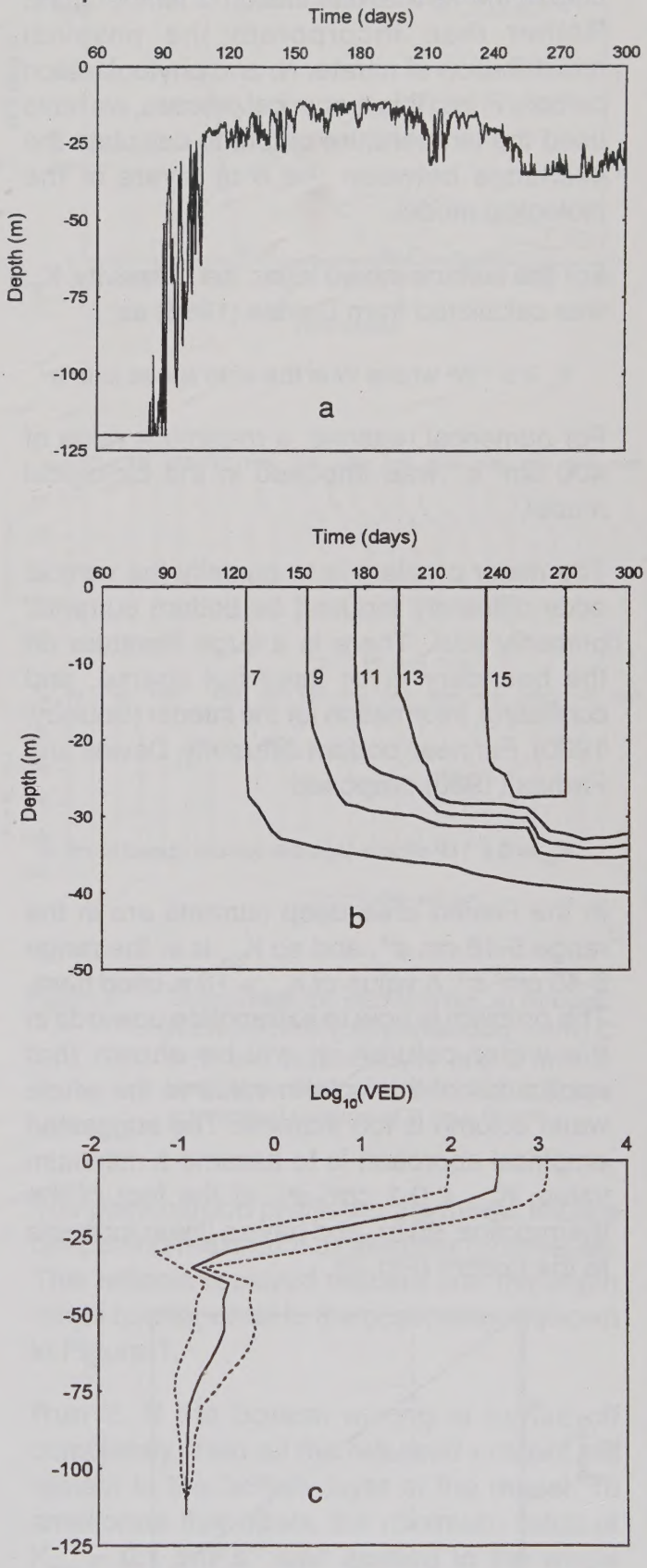


Figure 2 Output from the PWP model simulation for 1976. a) Mixed layer depth; b) temperature/depth distributions; and c) vertical eddy diffusivity values calculated from the temperature distributions.

The PWP model calculates the vertical flux of heat by an iterative process and has, as one output, the vertical distribution of temperature. Rather than incorporate the physical redistribution of nitrate, N, and phytoplankton carbon, P, into this numerical process, we have used the temperature output to calculate the exchange between the 5 m layers of the biological model.

For the surface mixed layer, the diffusivity, K_0, was calculated from Davies (1986) as:

$K_0 = 3 * W^3$ where W is the wind speed in m s^{-1}

For numerical reasons, a maximum value of 400 cm^2 s^{-1} was imposed in the biological model.

The major problem is to quantify the vertical eddy diffusivity induced by bottom currents, primarily tidal. There is a large literature on the boundary layer itself but sparse, and conflicting, information for the interior (Soulsby, 1990). For near-bottom diffusivity, Davies and Furnes (1980) proposed:

$K_{bot} = 0.2 * U^2$ where U is the current speed in cm s^{-1}

In the Fladen area deep currents are in the range 5-15 cm s^{-1}, and so K_{bot} is in the range 5-45 cm^2 s^{-1}. A value of $K_{bot} = 10$ is used here. The problem is how to extrapolate upwards in the water column. It will be shown that application of the bottom value to the whole water column is too extreme. The suggested empirical approach is to assume a minimum value, $K_{min} = 0.1$ cm^2 s^{-1}, at the foot of the thermocline, 60 m, and have a linear increase to the bottom (Fig. 3).

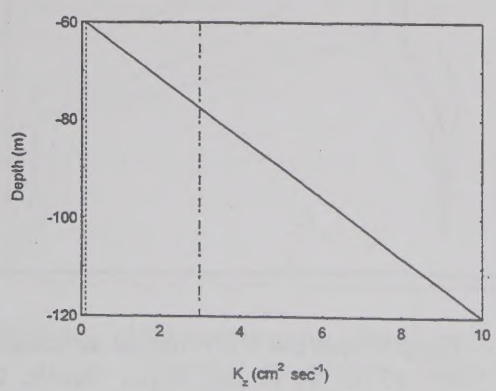


Figure 3 Three simulations of vertical eddy diffusivity; the standard run (solid line); low K_z (dashed line); and high K_z (dotted-dashed line).

Biological processes

The biological model (see Appendix) is a simplified version of the multi-layer system described in Steele and Henderson (1976). This model incorporates cohort structure for the herbivorous zooplankton but the details of this process and its consequences for the model are described elsewhere (Steele and Henderson, 1995). Note that removal of the herbivores by predation assumes that the predator population varies in proportion to the herbivore biomass, H (Steele and Henderson, 1992).

The only nutrient considered is nitrogen and no distinction is made between the new and recycled forms. A fixed carbon to nitrogen ratio of 7 is assumed for uptake, body burden, and excretion. Thus the model can be run in either unit.

The general cycling of nutrients into, within, and out of a layer (Fig. 4) shows the significance of vertical transport of faecal pellets to the bottom. Sinking rates of phytoplankton vary with size and senescence (Smayda, 1970). Following Steele and Yentsch (1960), it is assumed that sinking rate varies with ambient nutrient concentration in the range 0.2-1.0 m d^{-1}. Grazing rate is assumed to be equal at all depths in the range 0-100 m.

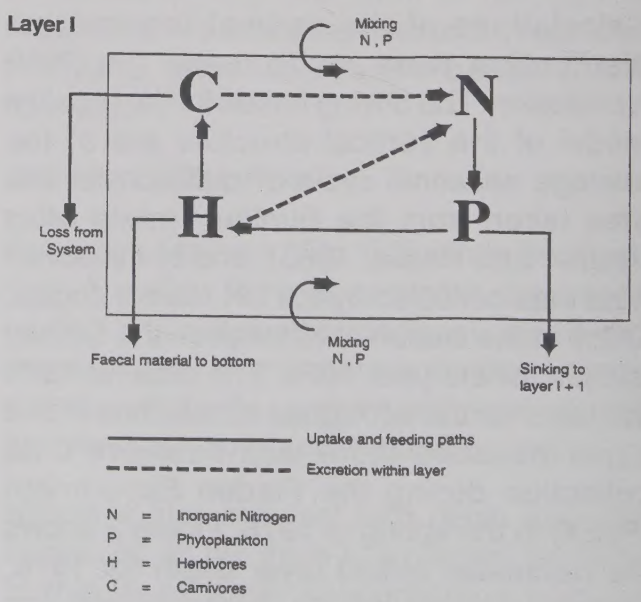


Figure 4 Nitrogen pathways in each layer where N = inorganic nitrogen, P = phytoplankton, H = herbivores, and C = carnivores.

Simulations

The empirical solution to the technical problems of introducing benthic turbulence is illustrated by three simulations. The "standard" run will be shown first and then the alternative mixing patterns. The values for the parameters are given in the Appendix.

Run 1 assumes a) K_{bot} = 10 cm^2 s^{-1}; and b) K_{min} = 0.1 cm^2 s^{-1} and that Kz is linear in the depth range 65 m to 115 m. The simulation is run for 240 days, starting on calendar day 61 and ending on calendar day 300 (approximately March to October inclusive). The initial conditions are N = 8 mmol N m^{-3}, P = 5 mg C m^{-3}, and H = 12 mg C m^{-2} which is divided into 12 cohorts of adult *Calanus* spp that recruit at five day intervals.

The peak value for P (Fig. 5a) of about 530 mg C m^{-3}, would correspond to a chlorophyll concentration of about 12 mg m^{-3}. This is about twice the observed value in 1976, although concentrations greater than 20 mg m^{-3} have been found in other years. The peak value for H converts to 3 mg dry weight m^{-2} and this is close to the observed maximum. A better test is obtained by comparing the cohort structure in the model with field data (Krause and Trahms, 1983). The comparison is described in Henderson and Steele (1995).

On this basis we shall now focus on the depth distributions (Fig. 5b,c). The nutrient profiles have the correct general shape as shown in the observations (Fig. 1). However the uniform lower layers extend up to 60 m in mid-summer whereas the observations suggest this level is closer to 75 m. This divergence corresponds to the differences between observed and calculated temperature profiles and suggests that further modifications to the bottom-induced mixing regime would be desirable.

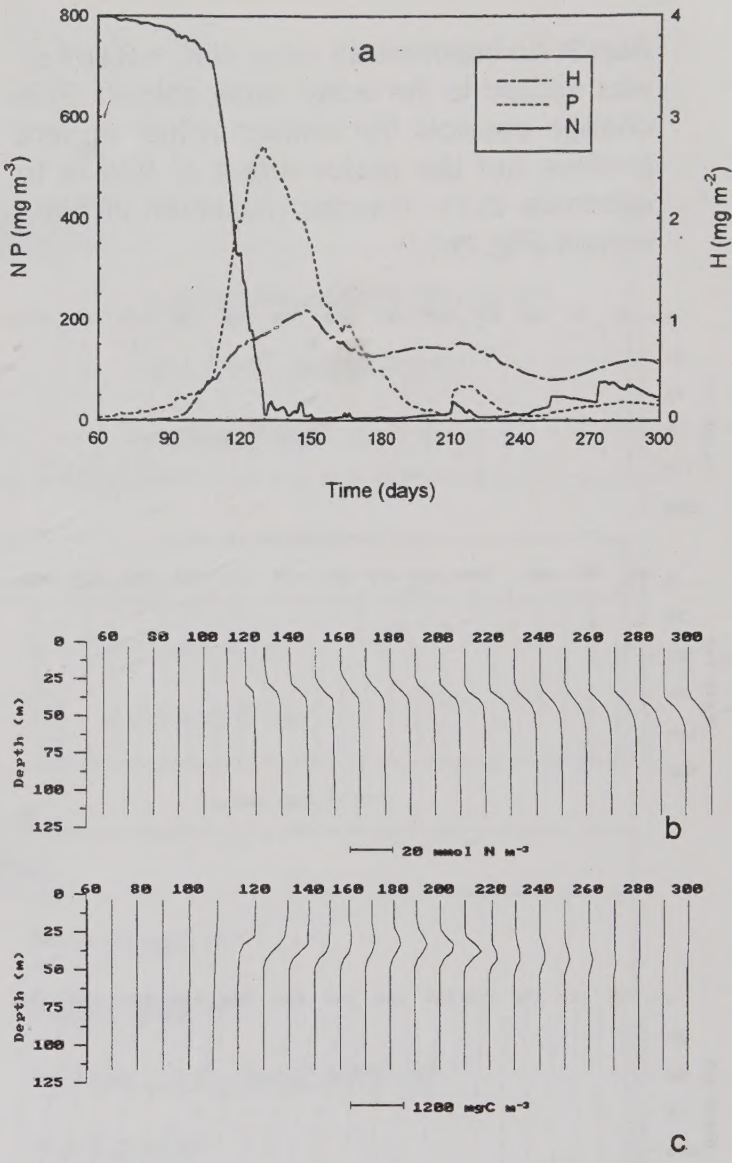
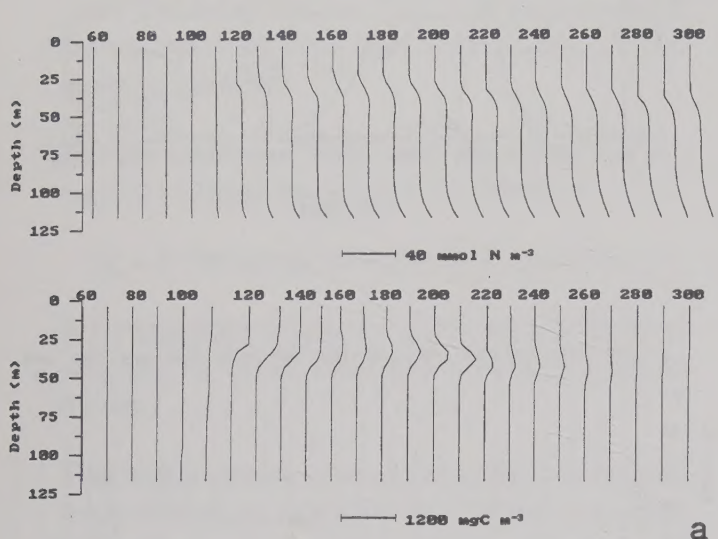


Figure 5 Output from the standard run. a) nitrogen, N (mmol N m^{-3}), phytoplankton, P (mg C m^{-3}), and herbivores, H (mg C m^{-2}); b) vertical profiles of N (mmol N m^{-3}); and (c) vertical profiles of P (mg C m^{-3}).

The plant carbon profiles in the model show a deepening maximum as summer progresses. This reflects received wisdom and the depth range corresponds to the observations shown in Figure 1.

Run 2. If the bottom mixing is turned off completely, then all the released nutrient will remain in the bottom layer of the model. To ameliorate this effect, the minimum value of K_{min} = 0.1 cm^2 s^{-1} was applied to the whole water column (Fig. 6a). The mid-water maximum is retained but the nutrient profiles are quite unlike observations (Fig. 1). This is the primary evidence of the need for bottom-generated diffusion.

Run 3. An intermediate value of $K_z = 3$ cm^2 s^{-1} was applied to the entire water column. This change corrects the artifact in the nutrient profiles but the major effect of this is to eliminate the mid-water maximum in plant carbon (Fig. 6b).[1]



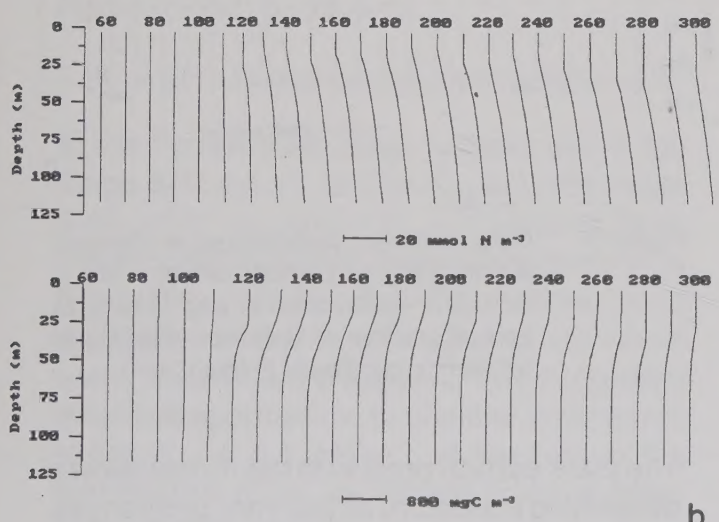


Figure 6 Vertical profiles of N and P with added diffusivity at all depths. a) 0.1 cm^2 s^{-1}; and b) 3.0 cm^2 s^{-1}.

The output from Runs 2 and 3 form the basis for using a bottom-generated diffusivity which decreases with height above bottom. It is unlikely that a linear decrease above the bottom is correct. There are a variety of alternative forms (eg van Aken, 1984; Davies, 1986; Soulsby, 1990). The tidally induced diffusivity would be expected to depend on the density gradient as well as the shear. Thus it will interact with the surface-driven stability distribution.

Decreasing depth and increasing tides determine the vertical stratification (Simpson and Hunter, 1974). But such changes also affect the nutrient supplies. Although it is an artificial example, it is relevant to note the changes in the overall cycles of N, P, and H, with increased "tidal" mixing (Fig. 7). These variables now follow the seasonal radiation rather than the stratification and resemble cycles in shallow or inshore waters, without the spring outburst usually observed offshore (Fig. 5a). This is a further reason to require the form of mixing in Run 1.

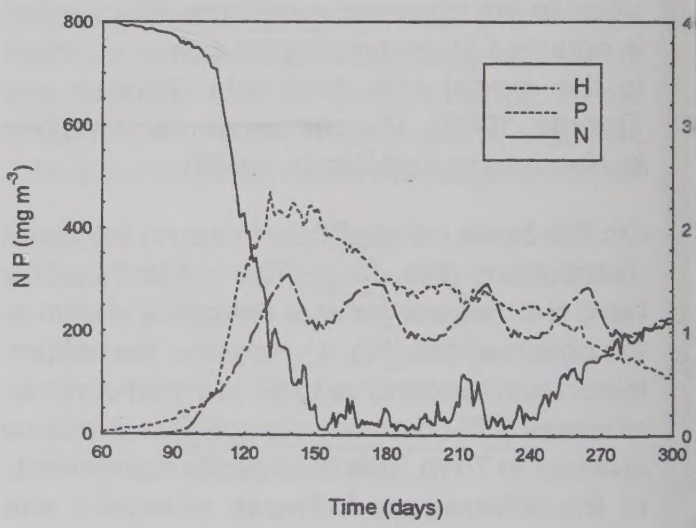


Figure 7 Seasonal cycles of N, P, and H for the higher mixing rate in Figure 6b.

1 The high mixing rate would be likely to remove a chlorophyll peak due to variable chlorophyll to carbon ratios.

Table I

Model parameters

Physical		
Surface PAR	RAD0	varies between 20-200 W m^{-2}
Attenuation	ATT0 = 0.1	with no phytoplankton
	ATTP = 0.0005*P	(where P is in mgC m^{-3})

Nutrient	
Half saturation concentration	A = 0.2 mmol N m^{-3}
Initial nitrate concentration	N0 = 8.0 mmol N m^{-3}

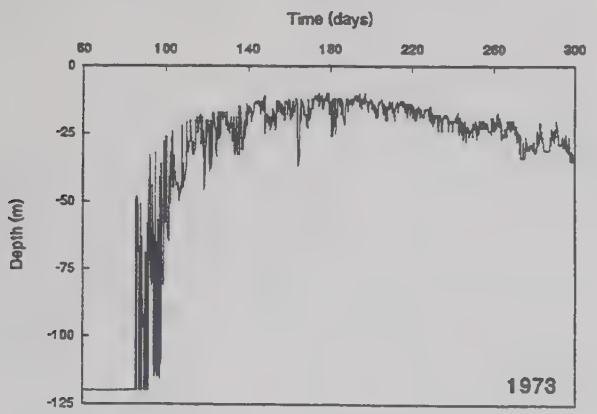
Phytoplankton	
Initial phytoplankton concentration	P0 = 5 mgC m^{-3}
Maximum photosynthesis rate	PMAX = 0.5 d^{-1}
Low light growth	ALPHA = 0.04 (mgC m^{-3})$^{-1}$ d^{-1}
Maximum sinking rate	V = 1.0 m d^{-1}
Zero sinking at	NMAX = 10 mmol N m^{-3}
Respiration rate	RESP = 0.05 d^{-1}

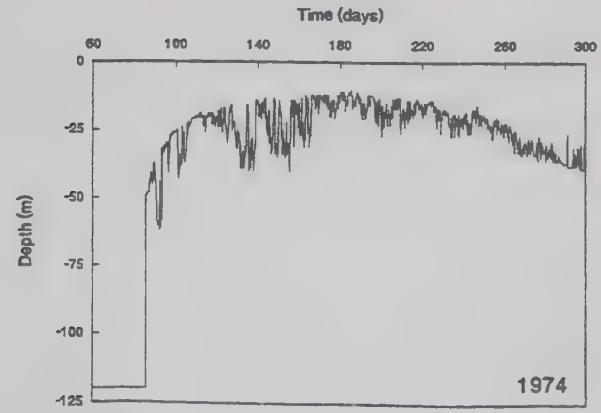
Zooplankton	
Half saturation grazing	B = 25 mgC m^{-3}
Maximum grazing rate	C = 1.0 d^{-1} (over the upper 100 m of the water column)
Fraction phytoplankton assimilated	ASS = 0.7
Fraction ASSimilated for growth	EFF = 0.6
Fraction PREDation excreted	EXC = 0.7
Predation rate	GX = 0.12

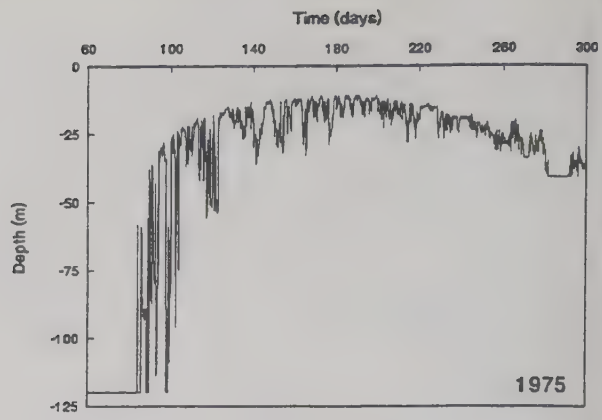
Discussion

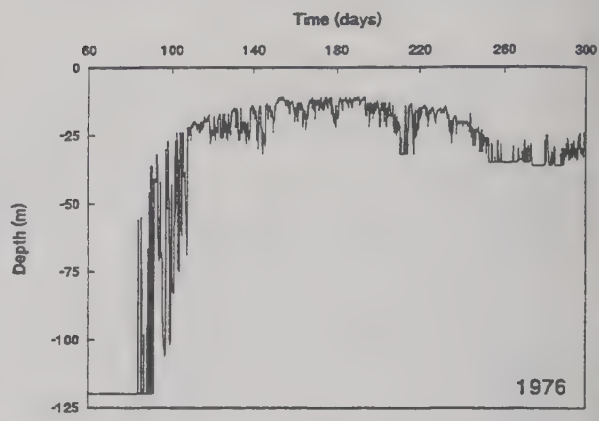
Technical and conceptual development of combined physical/biological simulations can result in a proliferation of parameters. For the biology especially, many of these do not have closely defined bounds. Thus simplicity may impose conceptual limitations but it provides useful constraints on model fitting. The ecological model used here is sensitive to variations in 12 parameters that represent the biological rate processes. In this model the values for the parameters (Table I) have been chosen to be within acceptable limits (eg Fasham *et al.*, 1990; Radach, 1983). An exception is the predation rate which is not well defined and so this rate, and this rate only, is used to tune each of the runs.

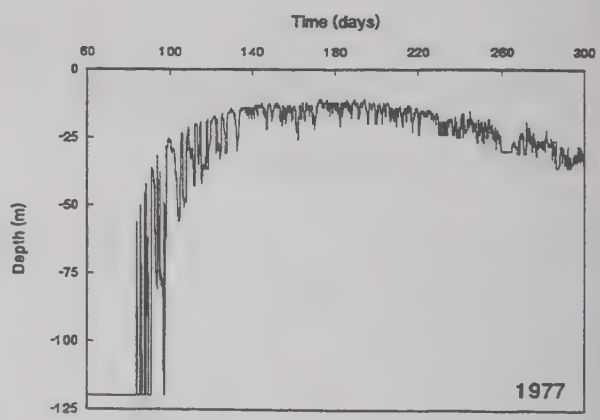
The physical rates are better known and the PWP model is considered a good simulator of the spring and summer thermal structure. The mixing rates, and consequent mixed layer depth, for 12 years of variable wind stress appear reasonable (Fig. 8). The smaller downward penetration of heat is probably a result of inadequate interactions between surface- and bottom-induced turbulence.

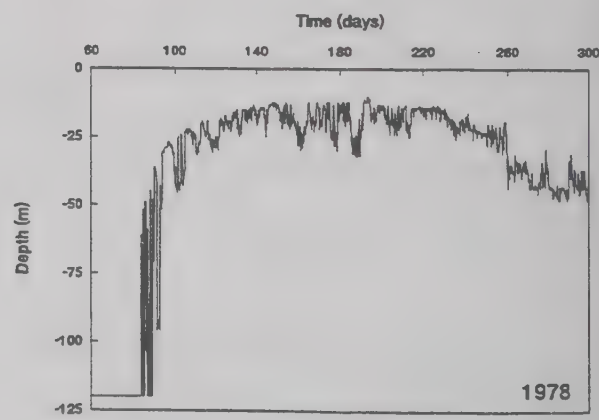


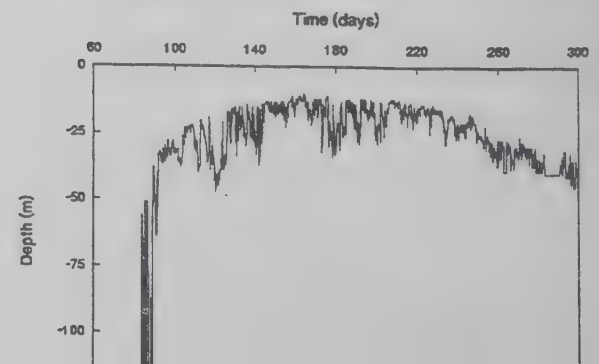












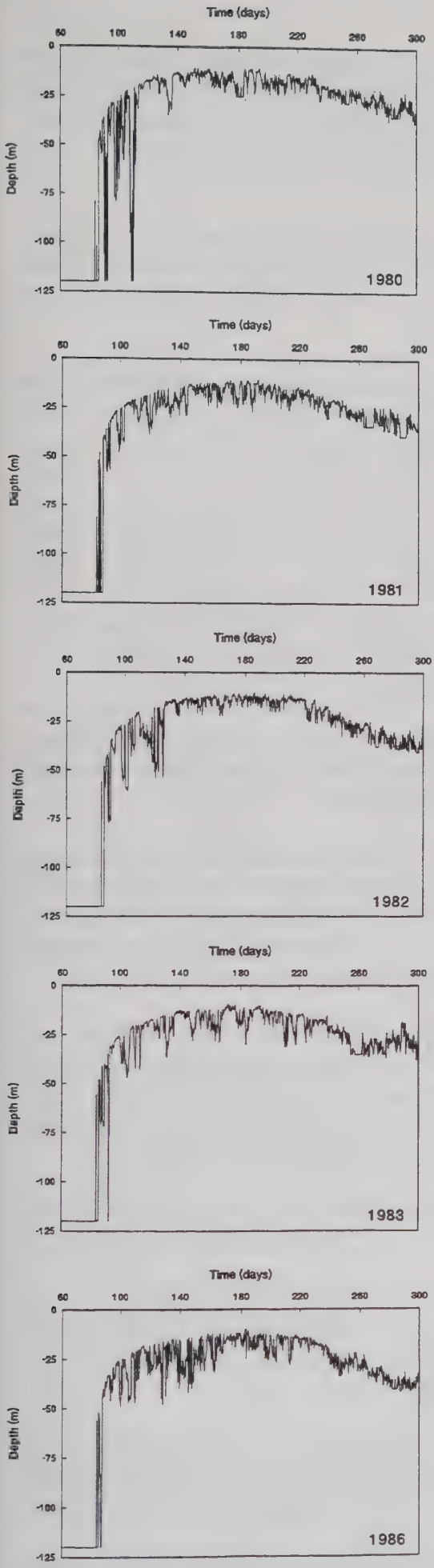


Figure 8 Simulations of mixed layer depth on the Fladen Ground for March to October in the years 1973-1983 and 1986.

The simulations used here indicate the ecological significance of mixing in the lower layers on the continental shelf. In particular the mid-water chlorophyll maximum provides a critical test of the physical model. The major lacuna is the mixing rate in the interior induced by tidally-generated bottom friction. Earlier models (eg van Aken, 1984; Davies, 1986) specify an upper and lower mixed layer but do not capture detail in the thermocline. The vertical eddy diffusivity at the top of the boundary layer is an important parameter and may be estimated very approximately. The exact value may not be critical so long as it is relatively large.

The critical parameter is the value, K_{min}, for mixing at the base of the thermocline. With the present assumptions, $K_{min} > 0.3$ removes the mid-water maximum. A value of $K_{min} < 0.03$ results in a severe decline in production rate after August. The relation of K_z with depth above the boundary layer is not known, and so it is difficult to be more precise about an empirical value for K_{min}.

The impact of benthic turbulence on mid-water structure is well known. Simpson and Hunter (1974) showed the significance of the stratification parameter, h/u^3 (where h = water depth, and u = rms tidal current speed), in determining the position of fronts which separate stratified from well-mixed regions. However, to our knowledge, there is no theory that extends the effect of these two variables - tide and depth - into the stratified region. It is likely that the benthic mixing component will be decreased by stability in the water column and this could determine the value for K_{min}. But this mixing will itself alter the stability derived from surface heating. Thus the two processes - surface and bottom - will be highly interactive and not simply represented by addition. These interactions may be the reason why the observed temperature and nutrient profiles are more diffuse than the simulations.

Further technical development will depend on the ability to produce interactive models. These interactions become increasingly important for the biology as simulations of shallower but stratified areas are considered. Increased mixing in the thermocline will result in higher

yearly production of phytoplankton and zooplankton (Steele, 1974). But a comparison of Figures 5 and 7 show the shift from a spring phytoplankton maximum dependent on thermocline formation, to a summer maximum due mainly to tidal mixing. Thus, production in better mixed regions will not only be larger and at a different season but may also be more regular. In such regions the motions will be complex and a three-dimensional model is required (Soulsby, 1990).

Summary

Simulation of vertical physical structure induced by wind mixing is insufficient to produce realistic profiles of nitrate and chlorophyll in stratified waters on the continental shelf. The effects of turbulence at the benthic boundary must be introduced. The profile of mixing within the water column induced by this factor is critical for the nutrient and chlorophyll distributions. This report describes the development and testing of a model generating adequate vertical structure in these variables.

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Appendix

The model is run with 24 depth layers, each 5m thick. The equations for nitrogen, N, and phytoplankton, P, in layer I are:

$$\frac{\partial N}{\partial t} = - Prod + Reg + \frac{\partial}{\partial z}\left(K \frac{\partial N}{\partial z}\right)$$

$$\frac{\partial P}{\partial t} = Prod - Graz - Sink + \frac{\partial}{\partial z}\left(K \frac{\partial P}{\partial z}\right)$$

where the diffusion terms are calculated as exchanges (Fig 4) using the diffusion coefficients, K_z, calculated from the PWP temperature distributions with the bottom diffusion terms added.

The herbivorous copepods are divided into 12 cohorts (see Steele and Henderson, 1976 and 1995). However, for the purposes of this paper, the total biomass, Biom (mgC m^{-2}, is described by:

$$\frac{d(Biom)}{dt} = (Eff.\ Ass.\ Graz - Pred).Biom$$

where the summation is over the 24 layers. The terms are defined as:

$$Prod = Phot. \frac{N}{(A+N)} - Resp$$

$$Phot = Pmax\ (1 - exp\ (-Alpha. \frac{Rad}{Pmax}))$$

$$Rad = Rad0.exp(-Attn.z)$$

$$Attn = Att0 + AttP.P$$

$$Sink = \frac{(V.P)}{z}, \text{ calculated as a flux between layers}$$

$$V = VO.\ (1 - \frac{N}{Nmax}),\ N < Nmax$$

$$Graz = \frac{C.P}{(B+P)}$$

$$Pred = Gx.Biom$$

$$Reg = (1 - Eff).Ass.Graz + Exc.Pred$$

where the fraction not assimilated, (1 - Ass), is faecal material which goes to the bottom where its nitrogen is regenerated immediately into the bottom layer. The predators are assumed to excrete evenly throughout the water column.

For simplicity, temperature control of rate processes has been ignored here. The range, 6°C to 14°C, seasonally and vertically, would alter the rates by a maximum of ±40%. It is assumed here that these changes would not materially affect the conclusions.

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